

## Grassland-woodland transitions Special Feature

**Climate change will increase savannas at the expense of forests and treeless vegetation in tropical and subtropical Americas**José D. Anadón<sup>1,2</sup>, Osvaldo E. Sala<sup>1,3\*</sup> and Fernando T. Maestre<sup>4</sup><sup>1</sup> School of Life Sciences and School of Sustainability, Arizona State University, Tempe, AZ 85287, USA<sup>2</sup> Department of Biology, Queens College, City University of New York, Flushing, NY 11367, USA<sup>3</sup> South American Institute for Resilience and Sustainability Studies, SARAS<sup>2</sup>, Maldonado, Uruguay<sup>4</sup> Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Móstoles, 28933, Spain

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## SUMMARY

**1.** Transition areas between biomes are particularly sensitive to environmental changes. Our understanding of the impacts of ongoing climate change on terrestrial ecosystems has significantly increased during the last years. However, it is largely unknown how climatic change will affect transitions among major vegetation types.

**2.** We modeled the distribution of three alternative states (forest, savanna and treeless areas) in the tropical and subtropical Americas by means of climate-niche modeling. We studied how such distribution will change by the year 2070 by using 17 downscaled and calibrated global-climate models from the Coupled Model Intercomparison Project Phase 5 and the latest scenarios provided by the 5<sup>th</sup> Assessment Report of the IPCC.

**3.** Our results support the savannization of the tropical and subtropical Americas because of climate change, with an increase of savannas mainly at the expense of forests.

**4.** Our models predict an important geographical shift in the current distribution of transition areas between forest and savannas, which is much less pronounced in the case of those between savannas and treeless areas. Largest shifts, up to 600 km northward, are predicted in the forest-savanna transitions located in the eastern Amazon.

**5.** Our findings indicate that climate change will promote a shift towards more unstable states: the extent of the transition areas will notably increase, and largely stable forest areas are predicted to shrink dramatically.

**6. *Synthesis.*** Our work explores dimensions of the impact of climate change on biomes that have received little attention so far. Our results indicate that climate change will not only affect the extent of savanna, forest and treeless areas in the tropical and subtropical Americas, but also will: i) promote a significant geographical shift and an increase of the extent of transition areas between biomes, and ii) decrease the stability of the equilibrium between forest, savanna and treeless areas, yielding a more unpredictable system.

## INTRODUCTION

The Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) provides unequivocal evidence of ongoing climate change, which is characterized by an increase in temperature globally and important modifications in rainfall patterns (IPCC, 2013). Climate change will have major impacts on the structure and functioning of terrestrial ecosystems (Peñuelas *et al.*, 2013), and is already promoting important changes in the spatial extent and distribution of vegetation types worldwide (Gang *et al.*, 2013). Our understanding of the impacts of ongoing climate change on terrestrial ecosystems has significantly increased in recent years (see Parmesan (2006); Parmesan & Yohe (2003); Paruelo *et al.* (1995); Walther (2010) and Peñuelas *et al.* (2013) for reviews). In tropical areas, forests might retreat yielding more open savanna-like systems, a pattern particularly well identified for the Amazonian region (Franchito, Rao & Fernandez, 2012; Salazar, Nobre & Oyama, 2007; Zelazowski *et al.*, 2011). Climate-induced changes in vegetation types will have direct effects on the provisioning of ecosystem services for humans (MEA, 2003). Shifts from grasslands into woodlands results in a significant reduction in livestock production (Anadón *et al.*, 2014), which can be offset by an increase in carbon sequestration (Havstad *et al.*, 2007) and soil fertility (Eldridge *et al.*, 2011). The shift from forest to grassland can also have impacts on ecosystem services other than the provisioning of timber or food, **such as a decrease in carbon sequestration and regulation of climate** (MEA, 2003).

Biome transitions are areas of high socio-ecological interest for many reasons. These areas have a unique and high biological diversity at multiple levels (from genes to communities; see Kark & Van Rensburg (2006) for a review), and are areas of high conservation interest (Smith *et al.*, 2001; Smith *et al.*, 1997). These areas are also particularly sensitive to human

activities such as grazing (Hudak, 1999), and to important components of climate change such as the increase in precipitation intensity and rainfall variability predicted for many terrestrial ecosystems worldwide (IPCC, 2013; Meehl, Arblaster & Tebaldi, 2005). In this direction, rapid vegetation shifts in responses to recent changes in climatic conditions are already being detected in areas such as the Arctic tundra (Sturm, Racine & Tape, 2001), the Alps (Gehrig-Fasel, Guisan & Zimmermann, 2007) and the drylands of the Southwestern U.S. (Van Auken, 2009). Recent studies have highlighted how climate change drivers, such as an intensification of the rainfall regime, may favor the recruitment and expansion of woody plants in savannah ecosystems (Holmgren et al., 2013; Kulmatiski & Beard, 2013), a vegetation transition with major ecological effects on biodiversity, nutrient cycling and carbon sequestration in drylands worldwide (Eldridge et al., 2011). **As such, forecasting how vegetation in transitional areas will respond to climate change is an urgent ecological question that has been poorly studied to date.**

Understanding how climatic variables such as rainfall and temperature determine woody vegetation cover in grassland-woodland transition areas has been an area of active research in the last decades (Hirota et al., 2011; Sankaran et al., 2005; Staver, Archibald & Levin, 2011; Williams et al., 1996). Continental-scale analyses of tree cover in African savannas have found that mean annual precipitation largely limits the maximum cover of woody species, and that disturbance dynamics control savanna structure below this maximum (Sankaran et al., 2005). More recent analyses have reported the presence of three alternative stable states (forest, savanna, and treeless) in the world's savannas (Hirota et al., 2011). These authors found that the tree cover values characterizing savannas (~20%) and forests (~80%) were found over multiple rainfall conditions, suggesting that woody cover is not controlled by gradual increases in precipitation, and that there is a shifting probability of being in either of the three stable states

identified. The reverse side of this multiple stable state equilibrium is the existence of highly unstable tree cover values (~5% and ~60%) that can be then identified as transition areas between biomes. A key property of the findings reported by Hirota *et al.* (2011) is that any given locality will have a probability of being forest, savanna and desert according to their climatic characteristics, and thus they allow us to quantify how likely transitions between vegetation types are likely to occur. For example, in a locality with very high probability of being forest and low of being savanna or treeless, the probability of transition between vegetation states is very low. As a consequence, the uncertainty of the locality is very low since it is highly probable that it will be a forest. On the contrary, the uncertainty of a locality with similar and high probabilities of being forest and savanna (and low probability of being treeless) is very high, since it is very difficult to predict whether this locality will be a forest or a savanna. In localities of high uncertainty, small changes in tree cover due to human activities (e.g. fires, selective logging) might have a large effect on the system and promote the transition from one state to another. On the contrary, localities with low uncertainty are likely to be more resilient to human-induced changes to tree cover (Hirota et al., 2011).

While research conducted over the last decades has provided key insights to advance our understanding of the mechanisms driving grass/woody vegetation coexistence in savanna systems, and has improve our ability to predict their responses to climate change, no previous studies so far have explicitly evaluated how forest-savanna-treeless transitions will change under future climatic conditions at regional to continental scales (but see Huttyra et al. (2005); Salazar, Nobre & Oyama (2007); Salazar & Nobre (2010) for forest-savanna transitions). We aimed to assess forest-savanna-treeless transitions under climate change for the tropical and subtropical Americas; a region that is crucial for preserving global biodiversity (Myers et al., 2000),

regulating the Earth's climate (Gedney & Valdes, 2000), and that directly supports the livelihood of more than 700 million people. Our objectives were to: i) assess the climatic determinants of the occurrence of treeless vegetation, savannas and forest in the tropical and subtropical Americas, ii) predict the future extent and distribution under climate change scenarios of treeless vegetation, savannas and forest in that region, iii) evaluate how climate change will affect the distribution of the transition areas among them, and iv) assess how climate change will affect the uncertainty of the occurrence of different vegetation types. To achieve these objectives, we modeled the spatial distribution of grasslands and woodlands and their transition areas in the studied region using the alternative stable state framework provided by Hirota *et al.* (2011) and large-scale remote sensing and climate data, and employed the latest climate change scenarios provided by the 5<sup>th</sup> Assessment Report of the IPCC (Taylor, Stouffer & Meehl, 2012) to forecast how such distribution will change by the year 2070.

## **MATERIALS AND METHODS**

### **Modeling the distribution of forest, savanna and treeless areas**

Our study area comprises the tropical and subtropical Americas, here defined as those areas between latitude 35°N and 35°S. Hirota *et al.* (2011) suggested that the different vegetation types in tropical areas, as described by tree cover, are actually alternative states, exhibiting sharp transitions between them at so-called tipping points. These authors identified three alternative states in the tropical areas of the Americas (forest, savanna and treeless areas) that were defined by the cutting levels of 5 and 60% of tree cover (i.e., treeless=0-5%, savanna=5-60%, forest=60-100%).

We modeled the distribution of the three states (forest, savanna or treeless) according to climatic variables by means of generalized linear models with a binomial distribution of errors, with the presence/absence of the state as independent variables, and with climatic descriptors (Mean annual temperature [T], Mean annual precipitation [P], T + P, P/T ratio and Aridity index [P/Potential evapotranspiration]) as independent variables. Our models rely on the understanding that climate governs the broadest outlines of distributions of species and biomes. This statement is well supported by current knowledge (see Araújo & Peterson (2012) for a review). In this sense, our models capture the main controls of biome distribution at a continental scale (i.e., climate), as shown by the high values of explained deviance obtained (see Results section).

Models were fitted to a random sample of 3000 2.5' x 2.5' (aprox. 4.5 x 4.5 km) cells from the study area. Tree cover percentage was assessed from the MOD44B Collection 3 product from MODIS (Hansen et al., 2003) originally at a 500 m resolution. 2.5 arc-minute resolution values were obtained by averaging the 500 m side cells within each 2.5 arc-minute side cell. Average tree-cover values were then transformed to a categorical map describing the three alternative states in the present time, using the 5% and 60% cutting levels described above. Mean annual precipitation, temperature and evapotranspiration were also assessed for each 2.5 arc-minute side cell. Precipitation and temperature were obtained from Worldclim database ([www.worldclim.org](http://www.worldclim.org); Hijmans et al. 2005). Evapotranspiration was obtained from the Global Potential Evapo-Transpiration (Global-PET) dataset (<http://www.cgiar-csi.org/>). Both databases describe climatic average values of the period 1950-2000 and are available at a 2.5 arc-minute resolution.

Eleven candidate models were fitted to the MOD44B data, including linear and quadratic responses to the different climatic descriptors (Table 1). Models for each state were ranked

according to the Akaike Information criterion (Burnham & Anderson, 2002). In accordance with previous works showing that tree cover and climate relationships at the continental scale are insensitive to the spatial resolution (Staver, Archibald & Levin, 2011), our results at 2.5 arc-minutes resolution were very similar to those obtained using a 30 second (aprox. 1 km) resolution (data not shown). We used the Global Land Cover 2000 (GLC2000) map to filter out areas undergoing human activities (categories 16-18 and 22; (Bartholome & Belward, 2005) from our analyses. **These areas cover  $5.1 \times 10^6 \text{ km}^2$ , comprising 23% of our study area (Fig. S1).** By only using natural areas, we maximize the decoupling of climate and land-use controls on the dynamics of biomes and their transitions areas. As such, our predictions are based solely on climatic controls and are largely independent of land-use change.

As it will be detailed in the Results section, a global model (i.e. including all the study area) for forest and treeless states presented high explanatory power ( $D^2 > 40\%$ ; Table 1). For the savanna state, however, the best global model according to the Akaike Information criterion performed poorly ( $D^2 = 12\%$ ; Table 1), suggesting spatial non-stationarity (i.e. the response of the savanna state to climatic condition changes within our study area). To obtain a more robust model, and starting from the best global model ( $P^2 + T^2$ ; Table 1), we developed models with a spatial factor describing different subareas within our study area. This factor was included as an interaction term in the models. Because of the latitudinal organization of macroclimatic control and major biomes on the Earth (Bailey & Ropes, 1998), this factor divided our study area latitudinally in two or three areas. Since we did not know which areas were a priori responsible for the presence of non-stationarity in our data, we fitted models with different spatial factors describing all possible two and three latitudinal subareas within our study area. To make the number of latitudinal subareas tractable, the minimum latitudinal width of the subareas were  $5^\circ$



(for example from 15°N to 20°N, see Table S1 in Supporting Information for examples of factors including different latitudinal subareas). In total we fitted 91 models, each one including the best global model and a spatial factor. As detailed in the Results section below, a large number of models had a very similar explanatory power (Table S1, Supplementary Information). Hence, the model for the savanna state was built using a weighted average consensus approach (Marmion et al., 2009). For doing so, we first selected a subset of models with the highest accuracy, and then calculated a weighted average according to a model performance metric (Hartley, Harris & Lester, 2006; Marmion et al., 2009). In our case, and given the differences in the explanatory power of the models, we selected the 20% best models according to their explained variance ( $n = 18$  models, range of explained variance of these models = 27.6-33.6%). Models were weighted according also to their explained deviance (Araujo et al. 2007). We did not use the Akaike weights (Burnham & Anderson, 2002) for model averaging because this approach led us to the selection of only one best model (i.e. weight of the first ranked model = 0.996).

Our distribution models for forest, savanna and treeless areas were projected to the study area using present conditions (1950-2000) and climate change scenarios. For the scenarios, we used 17 downscaled and calibrated global climate models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Taylor, Stouffer & Meehl, 2012) (See Table S2, Supplementary Information). We selected for our projections the Representative Concentration Pathway 8.5 (RCP8.5) for the year 2070. Within the Fifth IPCC Assessment Report, RCP8.5 represents the scenario with the highest concentration of greenhouse gases, and with a predictive radiative forcing of  $+8.5\text{W/m}^2$  (IPCC, 2013). Our rationale behind the selection of the worst (but possible) scenario is that we are more interested in capturing the overall directions of the changes than in quantifying exactly the extent of the changes. To describe the extent of forest, savanna

and treeless areas in the present time and for the year 2070, each cell was assigned to the state with largest probability of occurrence.

## **Modeling transitions**

Our study system is comprised by three states (forest, savanna and treeless areas) and two possible transitions (forest-savanna and savanna-treeless). To model these two transitions, we first divided our study area in the forest-savanna and savanna-treeless systems. These two subareas are mutually exclusive. The forest-savanna system is defined as those areas where the probability in the present time of being savanna or forest is larger than the probability of being treeless. Conversely, the savanna-treeless system is defined as those areas where the probability of being savanna or treeless in the present time is larger than the probability of being forest (Figs. 2 and 3). Starting from the distribution maps of the three alternative states for the present time and the climate-change scenario of the 17 CMIP5 global climate models, we calculated transition maps between forest and savanna, and between savanna and treeless areas for these two periods. In the transition maps, we calculated for each cell a transition index ( $Trans_{AB}$ ) calculated as  $Trans_{AB} = p(A) - P(B)$ , where  $P(A)$  and  $P(B)$  are the probability of being in state A and B, as described by the distribution maps. The transition index ranges between 1 and -1, with 1 being those cells with the largest probability of being in state A and least probability of being in state B, and -1 the other way around (maximum probability of being in state B and least of being in state A). Values close to 0 indicate high uncertainty, being difficult to predict whether the cell will be in state A or B, and cells with  $Trans_{AB}=0$  are those that have exactly the same probability of being in state A or B, according to their climatic conditions. From the transition maps we identified transition areas, i.e. areas with the highest uncertainty, which were defined as those

with  $Trans_{AB}$  absolute values below 0.2. In the same vein, we defined the core areas of the biomes, i.e. areas with the lowest uncertainty, as those with  $Trans_{AB}$  absolute values above 0.5. The modeling approach described above was performed for each one of the 17 CMIP5 global climate models. Final projection maps for biome distribution, transition areas and their changes were built from the ensemble mean of the projections provided by the 17 models (Araújo & New, 2007).

## RESULTS

For the three states considered, the models with the largest values of explained deviance were those including temperature and precipitation (Table 1). The best models for forests and savannas included both variables with their quadratic terms, whereas for treeless areas the best model included the linear term of precipitation and the quadratic term of temperature. For forest and treeless states, a global model (i.e. including all the study area) presented high explanatory power ( $D^2=45$  and 60% for forest and treeless areas, respectively). As noted in the Methods, the global model performed poorly for savanna ( $D^2=12\%$ ). Models considering a spatial factor with multiple subareas had larger explanatory power for this area ( $D^2$  values ranging from 15.4% to 33.7%; Table S1). The consensus model for this state resulting from the ensemble modeling presented an averaged explained deviance of 30.3% (Table 1).

Our results indicate that forests will decrease in area in favor of savannas by the year 2070 under the RCP8.5 climate change scenario (Table 2 and Fig. 1). Forest areas are predicted to lose  $1.5 \pm 0.9 \times 10^6$  km<sup>2</sup>. This biome is expected to cover  $22 \pm 4\%$  of our study area in year 2070, which means a 24% (range 9-39%) reduction in comparison to its current distribution. Results from the 16 out of 17 CMIP5 global climate models indicated a reduction of forest area

(Table S3). The general agreement shown by the projections of each one of the 17 CMIP5 global climate models in relation to changes in forest area indicates that our predictions are robust regarding uncertainties of the global climate models (Table 2). Changes in extent of treeless areas are predicted to be of small extent ( $-24 \pm 178 \times 10^3 \text{ km}^2$ ). Results from 8 CMIP5 climate models predicted a reduction, whereas 9 models show an increase in treeless areas. This limited change actually means that the percentage of the tropical and subtropical Americas covered by treeless areas might not vary significantly due to climate change. As it will be discussed below, this result does not mean that treeless areas might remain stable, but that the extension of some treeless areas might be compensated by the contraction of others.

For the forest-savanna system, the largest transition area is located in the southern portion of the Amazonian rainforest (Figure 2). Comparatively, minor transition areas are located north of the Amazonian forest and along Central America. Within the savanna-treeless system, main transition areas are located in the southern border of the North American deserts and along Pacific coast in South America (Fig. 3). Our predictions indicate that, within the forest-savanna system, changes in the multistate equilibrium toward savanna occur mainly in the East Amazonia and North Matto Grosso regions (Fig. 4). Within the savanna-treeless transition realm, changes towards savanna occur in the Peruvian and Bolivian slopes of the Andes facing west, north of the Atacama Desert. Despite the overall reduction of the total forest area, our models predict an increase in the probability of forest in the southern Atlantic Forest region. Shifts towards treeless areas are of much lesser extent and intensity (i.e. amount of change in the transition index) than those towards forest or savanna. Main areas where our models predict a shift towards treeless areas are Northeastern Brazil and part of the Chaco, between Paraguay and Bolivia.

Our models predict an important geographical shift in the current distribution of the forest–savanna transition, which is less pronounced in the case of the savanna-treeless transition (Fig. 5). The largest move in forest–savanna transitions (up to 600 km westward) occurs in the eastern part of the Amazon, affecting the contact areas of the Amazon with three different savanna systems present in the region (Llanos, Roraima and Cerrado). Lesser shifts (up to 100 km northward) occur in the southern limit of the Amazonia. Regarding the savanna-treeless transition line, our models predict minor shifts (up to 50 km westward) in the arid and semiarid areas of West South America (i.e., Atacama, Chaco, Monte Desert). Our models suggest that the shift in the transition line in this area increases towards the South, being maximal in the Argentinean Monte Desert. Transition areas located in the North American deserts (i.e. Mojave, Sonoran, Chihuahuan) are not expected to shift (Fig. 5).

Changes in the extent and geographical location of the transition areas occur simultaneously with an increase of the uncertainty of the system state (Fig. 6). In the forest-savanna system, the reduction of forest areas is at the expense of those areas with current lowest uncertainty of being forest. A large fraction (58%) of these areas, which can be considered the core of the forest biome, shift towards areas with higher uncertainty levels (Fig. 6). As a result, core forest areas, which nowadays occupy  $3.1 \times 10^6 \text{ km}^2$ , are projected to cover  $1.3 \times 10^6 \text{ km}^2$  (range:  $0.3 - 2.4 \times 10^6 \text{ km}^2$ , Table S4). The different projections resulting from the 17 CMIP global climate models show consistent patterns in the changes in uncertainty of the forest-savanna system, as shown by the reduced standard deviation of the predictions (Fig. 6). All 17 CIMP5 climate models predict a reduction in the areas of low uncertainty of being forest (Table S4). Forest-savanna transition areas (i.e. those where the difference in the probability of being forest and savanna is  $<0.2$ ) increased on average by 32%, from  $2 \times 10^6 \text{ km}^2$  to  $2.7 \times 10^6 \text{ km}^2$

(range=  $2.2 - 3.6 \times 10^6 \text{ km}^2$ , Table S4). A similar pattern, but much less pronounced, occurs in the savanna-treeless system, with a decrease in areas with high certainty of being treeless that shift towards areas of higher uncertainty (Fig. 6 and Table S5). The largest increases in uncertainty of the system state, projected to occur on the forest-savanna system, are located around two areas: the Amazon forest, particularly in the west, and the southern portion of the Atlantic Forest, because of their shifts towards savanna and forest, respectively (Fig. 7). The largest decreases in uncertainty are located in those savanna areas on the West of South America (Llanos, Roraima, Northern Cerrado), which are clearly expected to shift towards savanna.

## DISCUSSION

~~Transitions between forests, savannas and treeless are of utmost importance for understanding major environmental issues such as desertification (Maestre et al., 2009; Schlesinger et al., 1990) and the global carbon cycle (Pacala et al., 2001), and have important socio-economical and management implications at large scales (Gifford & Howden, 2001; Hudak, 1999; Van Auken, 2009). Despite the importance of this topic, no previous study has evaluated how climate change will affect these transitions areas at regional to continental scales.~~ Our results indicate that climate change according to the RCP8.5 scenario of the IPCC will promote the savannization of the tropical and subtropical Americas, with an increase of savannas mostly at the expense of forests. Such change will also increase the extent of transition areas between savannas and forests, and will promote a dramatic reduction of stable forest areas. According to current knowledge, the shifts predicted in the distribution and stability of transitions areas are expected to bring important changes to the biota and the provision of ecosystem services such as C sequestration, climate regulation and food production in one of the most important regions worldwide for biodiversity and human wellbeing (MEA, 2005).

Our modeling approach, which relies on niche modeling theory and focuses exclusively on the climatic controls of transitions, does not take into account other factors that have been identified as interacting with climate drivers, such as feedbacks between tree cover and climate, particularly in the rainforest (Coe et al., 2013; Malhi et al., 2008), sea surface temperature (Pereira, Costa & Malhado, 2013), CO<sub>2</sub> fertilization (Lapola, Oyama & Nobre, 2009) and land uses (Nepstad et al., 2008). In the same vein, our models use average annual values, and do not consider intra- and inter-annual variability in rainfall and temperature, which have been described to have significant effects in driving tree cover (Holmgren et al., 2013; Malhi et al., 2008). Notwithstanding, the overall agreement (discussed below) between our projections and those obtained by previous studies using more complex models regarding the direction, spatial location and order of magnitude of the vegetation changes observed at a regional scale makes us confident on the results reported here. ~~Furthermore, the relatively reduced variability of the projections obtained from each one of the 17 CMIP5 global climate models used also indicates that our predictions are robust regarding the uncertainty of the models using the Representative Concentration Pathway 8.5 for the year 2070.~~

#### CLIMATE-CHANGE IMPACTS ON THE EXTENT OF SAVANNA, FOREST AND TREELESS AREAS

Our models predict that climate change will increase the extent of savannas in the Americas by 12% (range=5-19%, average increase= $1.5 \times 10^6 \text{ km}^2$ ) at the expense mostly of forests, which will decrease by 24% (range= 9-38%, average decrease=  $1.5 \times 10^6 \text{ km}^2$ ) and in much less extent of treeless areas. Overall this result matches the process of savannization predicted for the area for the 21<sup>st</sup> century because of climate change (Franchito, Rao & Fernandez, 2012; Hutyra et al.,

2005; Cook & Vizzy, 2008; Salazar & Nobre, 2010). In agreement with previous results (Cook, Zeng & Yoon, 2012; Franchito, Rao & Fernandez, 2012; Hutyra et al., 2005; Salazar & Nobre, 2010), our projections indicate that major increases of savanna **will occur** at the expense of the Amazon rainforest, particularly at its south and southeastern portions. The amount of predicted reduction of forest, **ranging from 9% to 38%**, falls within the range predicted by other authors for South America (Cook & Vizzy, 2008; Hutyra et al., 2005; Salazar, Nobre & Oyama, 2007; Zelazowski et al., 2011). Previous studies have indicated that a larger stability of the forest in the Mata Atlantica in comparison with the Amazon under a climate-change scenario (Cook, Zeng & Yoon, 2012). Our results go one step further and predict a strong increase of the **probability of being forest** in this area. The forest of the Mata Atlantica is strongly fragmented, and only around 10% of its original area actually remains (Saatchi et al., 2001). Our findings indicate that in this region management actions designed to increase tree cover could take advantage of this positive inertia towards the forest.

In comparison with the transitions between forest and savanna, our prediction of transitions between savanna and treeless areas are overall small in extent, with a decrease of <1% of the treeless areas ( $2.4 \times 10^4 \text{ km}^2$ ). The impacts of climate change on the extent of drylands have been much less explored than those on forests, particularly in the Amazon region. Existing work indicates an overall increase in aridity and the extent of drylands in most the arid areas of tropical and subtropical Americas (Feng & Fu, 2013; Seager et al., 2007). Our results partially match these patterns, since they predict a general increase in the extent of the Caatinga (NE Brazil) and Chaco Seco (Argentina and Paraguay), and a patchy increase in the extent in North American deserts. However, against current knowledge (Feng & Fu, 2013), our models predict a



savannization of the Atacama Desert and particularly, of the Sechura Desert, along the Peruvian Pacific coast.

Changes in vegetation type from forest into savanna and treeless groups are expected to have major effects on climate (Oyama & Nobre, 2003; Shukla, Nobre & Sellers, 1990). Vegetation changes affect climate directly via changes in albedo and transpiration, the later mediated through changes in rooting depth. Vegetation changes also affect climate indirectly through changes in carbon cycling. Albedo increases along the gradient from forest, savanna to treeless vegetation therefore increasing the amount of radiation reflected back to the atmosphere and reducing surface temperature (Balling Jr, 1988). Rooting depth decreases from forest to treeless vegetation, reducing the depth of the soil explored by roots and functionally reducing the soil water-holding capacity (Jackson et al., 1996). A reduced soil-water capacity may decrease the latent heat therefore reducing the cooling capacity of the ecosystem. Finally, carbon storage is much larger in forest than in savannas and treeless vegetation in tropical areas (Saatchi et al., 2011), so the transition from forest into savanna may results in a net carbon emission into the atmosphere that will enhance climate warming.

## CLIMATE CHANGE EFFECTS ON TRANSITION AREAS AND THE STABILITY OF THE SYSTEM

Using the framework of alternative stable states provided by Hirota *et al.* (2011), we were able to project how the transition areas between biomes and the stability of the system are expected to change under climate change. These two related aspects have been much less explored than the changes in the extent of the biomes themselves. As with the projected changes in the extent of

biomes, shifts in the transitions between forests and savannas were much more pronounced than those between savannas and treeless areas.

Our models predict that climate change will promote a shift towards more unstable states, yielding **more uncertainty in system state**. Two aspects of this result deserve particular attention. On the one hand, the extent of the transition areas will increase by 32% on average (range=10-80%), and forest-savanna transition areas, now restricted to a thin belt between both biomes might become the dominant biome in large areas, particularly in the South and Eastern part of Brazil. On the contrary, large stable forest areas are predicted to decrease by 58% on average (range=23-90%). The climate control of vegetation types is strongest in the core (**i.e. ecological optimum**) of their distribution and weakens towards the edges (Sala, Lauenroth & Golluscio, 1997). It is in the edges of the distribution of vegetation types where other factors such as grazing intensity, fire, and logging become more important. The increase in uncertainty of large areas of the Amazon rainforest means that these areas will likely be less resilient to perturbations, and thus that they might be more sensitive to human management (Hirota et al., 2011). In these areas of high uncertainty, positive feedbacks might make that small changes in tree cover might induce a self-propagating shift to the alternative state (i.e. from forest to savanna or from savanna to forest). In this way, fragmented landscapes with a patchy distribution of forest and savanna might be more likely to turn into solely savanna landscapes, due to, for example, an increase in fire frequency and extent (Malhi et al., 2008). Interestingly, and as pointed out for the Mata Atlantica above, these feedbacks can also work in the opposite direction and, in areas of high uncertainty, tree cover increases due to habitat management are more likely to trigger the conversion of savanna to forest. Land-use changes are at present the main driver of the transition between states in the study area, particularly the conversion of forest to savanna

and treeless areas due to deforestation (Malhi et al., 2008). Overall, our results indicate that climate change will increase the importance of land use in shaping the extent of biomes during the next century.

## PREDICTED IMPACTS OF CLIMATE CHANGE ON BIODIVERSITY AND ECOSYSTEM SERVICES

The Amazon rainforest is a major component of the Earth's system, regulating Earth's climate (Malhi et al., 2008), and hosts up to a quarter of the world's terrestrial species (Barthlott & Winiger, 1998). Rapid transition from one vegetation type to another will certainly result in major biodiversity losses (Sala et al., 2005). Our models predict a shift of the forest-savanna transition area of up to 600 km in the eastern Amazon for year 2070. Given the magnitude and speed of this change, a pertinent question here is to what extent species will be able to keep pace with climatic changes to reach the equilibrium (Loarie et al., 2009). Although our understanding of colonization processes under climate change is still limited, current models indicate that species will lag behind projected climate shifts (Nathan et al., 2011; Prasad et al., 2013). The mismatch between climatic change velocity and colonization rates is expected to be exacerbated in flat reliefs (Loarie et al., 2009), which are dominant in the Amazonian Basin. In this area, our models predict the largest shifts from forest to savanna suggesting a high risk for species extinctions. However, as it has been described for tree species colonization after the ice caps retreated during the Holocene, isolated habitat patches outside the core distribution range of the biome could play key role in tracking climate change (Anderson et al., 2006; McLachlan, Clark & Manos, 2005; Parnucci et al., 2012). In our case, for example, small savanna patches currently

embedded in a forest matrix, could serve as colonizing source for the surrounding landscape when climate potentially in the area change from forest to savanna.

The portfolio of ecosystem services provided by forest, savannas and treeless vegetation types are drastically different. For example, savanna and grasslands in tropical and subtropical America constitute one of the main providers of food, particularly protein, of the world (FAO, 2007). As the reverse side of the ecosystem services linked to rainforest, predicted changes might have a positive impact on the provisioning of food (MEA, 2005). We predicted an increase in the extent of transition areas and in the uncertainty of the system. This means that alternative states (i.e. forest, savanna, treeless) are likely to be more evenly distributed at a small scale (i.e. a finer grain distribution) and that localities are expected to tip from one state to another more easily. As a result, ecosystem services provided at a local scale are likely to be more diversified but also more unpredictable, since larger portions of our study area might contain a combination of different biomes that will change more frequently. Food, timber, climate amelioration, clean water, recreation and conservation are ecosystem services that will be affected by vegetation transitions. These changes in the portfolio of ecosystem services resulting from vegetation transitions will affect different groups of stakeholders because they value ecosystem services differently.

## **Acknowledgements**

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(FP7/2007-2013)/ERC Grant agreement 242658 (BIOCOM). We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling, which is responsible for CMIP, and the climate modeling groups (listed in Table S2 of this paper) for producing and making available their model output. For CMIP the U.S. Department of Energy's Program for Climate Model Diagnosis and Intercomparison provides coordinating support and led development of software infrastructure in partnership with the Global Organization for Earth System Science Portals.

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## Figure Legends

**Fig 1.** Spatial projection of the three alternative states (forest, savanna and treeless areas) for the present time (1950-2000) and for the year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas.

**Fig 2.** Transition map for the forest-savanna system for the present time (1950-2000) and for the year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas. For the year 2070, the mean value of the 17 transition maps resulting from the 17 CMIP5 global climate models is shown. A histogram with the total amount of area of each class can be found in Fig. 6 (Top). The total area of each class for each one of the 17 transition maps resulting from the 17 CMIP5 global climate models can be found in Table S4.

**Fig 3.** Transition map for savanna-treeless system for the present time (1950-2000) and for the year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas. For the year 2070, the mean value of the 17 transition maps resulting from the 17 CMIP5 global climate models is shown. A histogram with the total amount of area of each class can be found in Fig. 6 (Bottom). Rest of legend as in Fig. 2.

**Fig 4.** Projected shift towards forest, savanna or treeless states for the year 2070 under the RCP8.5 scenario in the tropical and subtropical Americas. Shifts are estimated as the difference between the transition index in the present time and the year 2070 for the forest-savanna and the savanna-treeless systems. The mean value of the projected shifts for the 17 transition maps resulting from the 17 CMIP5 global climate models is shown. Beige area indicates those cells

where the change in the probability transition is below 0.1. Darker tones of green, red and blue indicate stronger shifts toward forest, savanna and treeless areas respectively.

**Fig 5.** Transition areas for the forest-savanna (left) and the savanna-treeless systems (right) in the present time and the year 2070 under the RCP8.5 scenario. For a given transition (i.e. forest-savanna), transition areas are defined as those cells in which the difference between the two alternative systems is less than 0.2. The mean value of the 17 transition maps for the year 2070 resulting from the 17 CMIP5 global climate models was used as base transition map.

**Fig 6.** Projected area under different classes of the transition index for the present (1950-2000) and under the RCP8.5 scenario for the year 2070 for the forest-savanna (Top) and the savanna-treeless transitions (Bottom). Forest-savanna transition index is calculated as  $p(\text{forest}) - p(\text{savanna})$ . Savanna transition index is calculated as  $p(\text{savanna}) - p(\text{treeless})$ . Values closer to 1 and -1 indicates lower uncertainty whereas values closer to 0 indicates higher uncertainty. Mean values and standard deviation of the 17 CMIP5 global climate models are shown. Results for each CMIP5 global climate model are shown in Figs. S4 and S5. Area in  $10^3 \text{ km}^2$ . Note that the total area of savanna is the sum of the savanna areas in both transition systems. The spatial representation of this histogram can be found in Figs. 2 and 3.

**Fig 7.** Changes in the uncertainty of the forest-savanna transition between the present (1950-2000) and the RCP8.5 scenario (2070) in the tropical and subtropical Americas. The change in uncertainty is calculated as the change in the transition index between the two projections (i.e. 1950-2000 and 2070). The mean value resulting from analysis of the 17 CMIP5 global climate

690 models is shown. Positive values of uncertainty indicate areas where the probability of tipping  
691 between forest and savanna will increase due to climate change.

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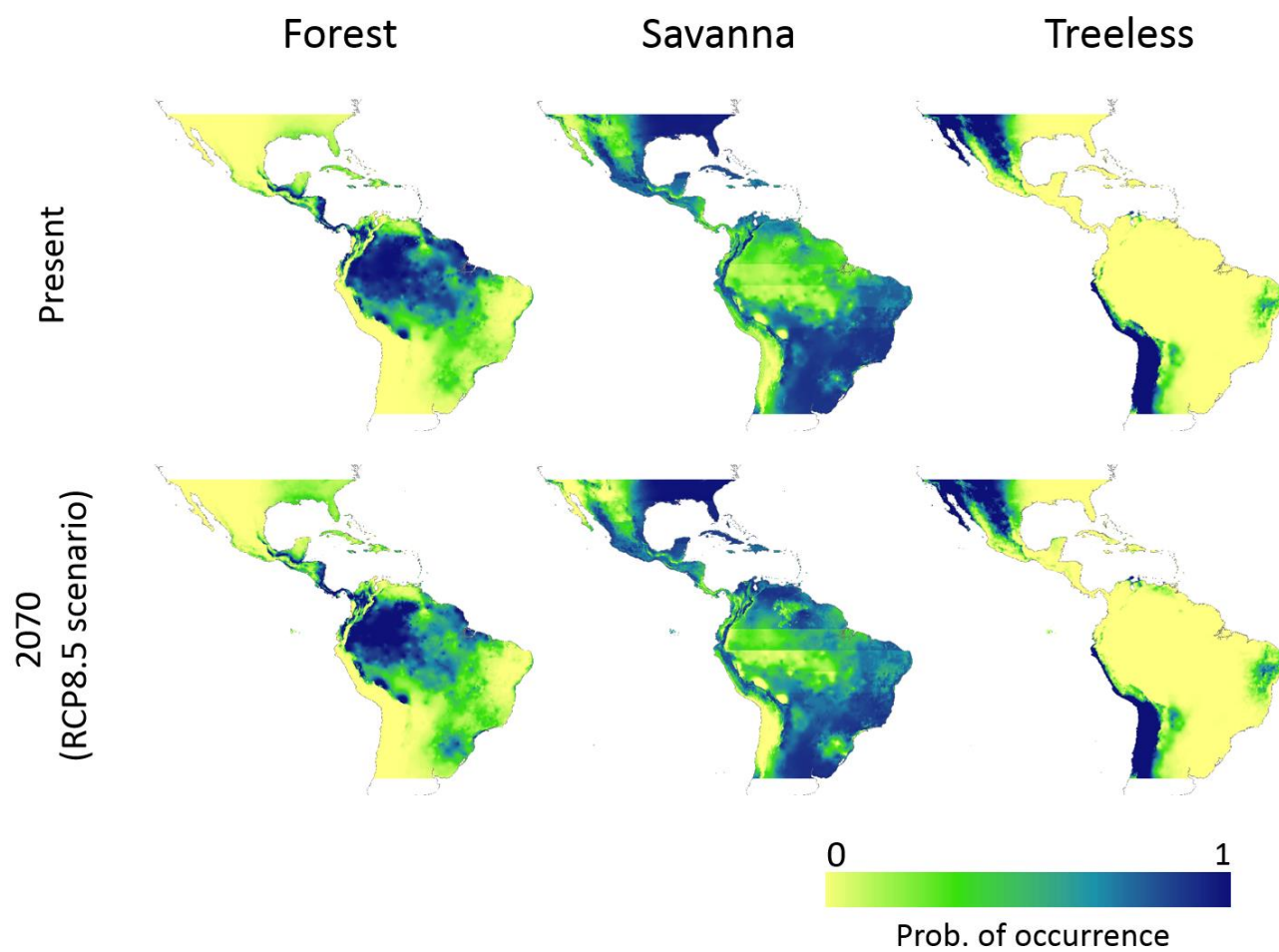
**Table 1.** Candidate climatic models fitted to the distribution of forest, savanna and treeless areas in the tropical and subtropical Americas. For each model, the explained deviance ( $D^2$ ) and Akaike Information Criterion (AIC) value are shown. For each state, the selected model is in bold. For the Savanna, the best global model (i.e, that with  $D^2 = 12.29\%$ ) was not used and the value in brackets represents the explained deviance of the model finally employed. In this case, the  $D^2$  value represents weighted mean of the  $D^2$  values of the 20% best multi-zone models (see Methods and Table S1 in Supporting Information). P=Mean annual precipitation; T=Mean annual temperature, ARIDITY=Aridity index (P/Potential evapotranspiration)

	Forest		Savanna		Treeless	
Model	$D^2$	AIC	$D^2$	AIC	$D^2$	AIC
P	39.30	2230.60	1.69	4029.92	65.02	946.43
P <sup>2</sup>	44.52	2041.20	10.35	3677.38	56.97	1165.07
T	24.79	2762.85	0.01	4098.74	28.05	1942.20
T <sup>2</sup>	24.81	2764.23	4.29	3925.37	29.37	1908.62
P <sup>2</sup> +T	45.64	2002.16	10.35	3679.19	56.79	1172.06
T <sup>2</sup> +P	41.76	2144.44	5.35	3884.16	<b>66.84</b>	<b>901.23</b>
P <sup>2</sup> +T <sup>2</sup>	<b>45.88</b>	<b>1995.36</b>	<b>12.29 (30.34)</b>	<b>3601.67</b>	56.97	1169.33
ARIDITY	32.38	2484.60	0.99	4058.49	58.97	1109.37
ARIDITY <sup>2</sup>	38.65	2256.38	4.02	3936.52	59.50	1096.95
P/T	15.30	3111.09	0.32	4086.00	27.80	1948.89
(P/T) <sup>2</sup>	33.02	2462.86	0.43	4083.42	-	-

**Table 2.** Projected representation of forest, savanna and treeless areas in our study area for the present time (1950-2000) and for 2070 under the RCP8.5 scenario. For the 1950-2000 period, real values (i.e. observed from the data, not modeled) are shown in brackets. Mean values and standard deviation from the 17 downscaled and calibrated CMIP5 global climate models are indicated. Results for each CMIP5 global climate model are shown in Fig. S3

	<b>1950-2000</b>		<b>2070 RCP8.5</b>		<b>Change</b>	
	<b>Area</b> ( $\times 10^3$ km <sup>2</sup> )	<b>%</b>	<b>Area</b> ( $\times 10^3$ km <sup>2</sup> )	<b>%</b>	<b>Area</b> ( $\times 10^3$ km <sup>2</sup> )	<b>Change (%)</b>
Forest	6235	29 (31)	4760 $\pm$ 896	22 $\pm$ 4	-1474 $\pm$ 896	-24 (-38 - -9)
Savanna	12765	58 (52)	14263 $\pm$ 921	65 $\pm$ 4	1498 $\pm$ 921	12 (5 - 19)
Treeless	2847	13 (17)	2823 $\pm$ 178	13 $\pm$ 1	-24 $\pm$ 178	-1 (-7 - 5)

**Fig 1.**

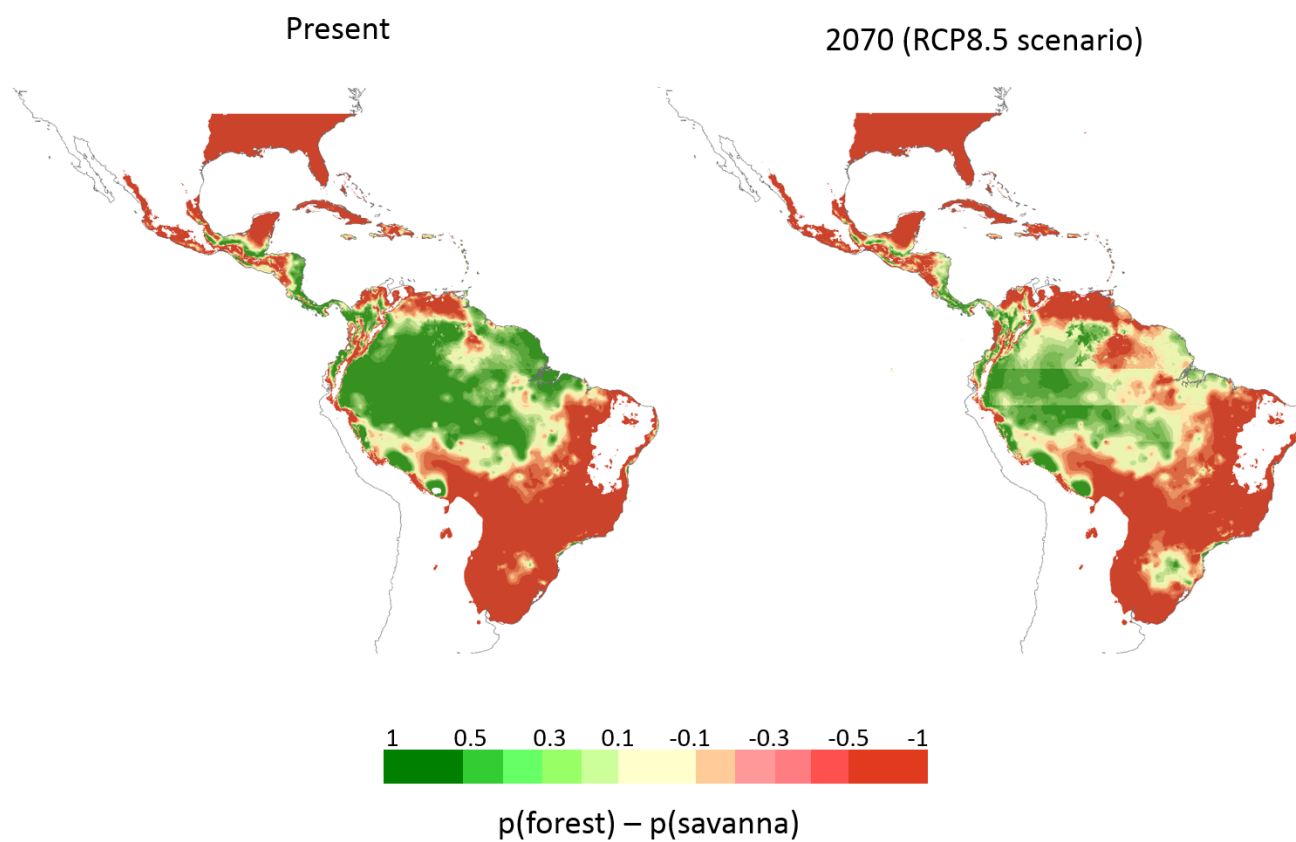


718 **Fig 2**

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## Forest-savanna transition



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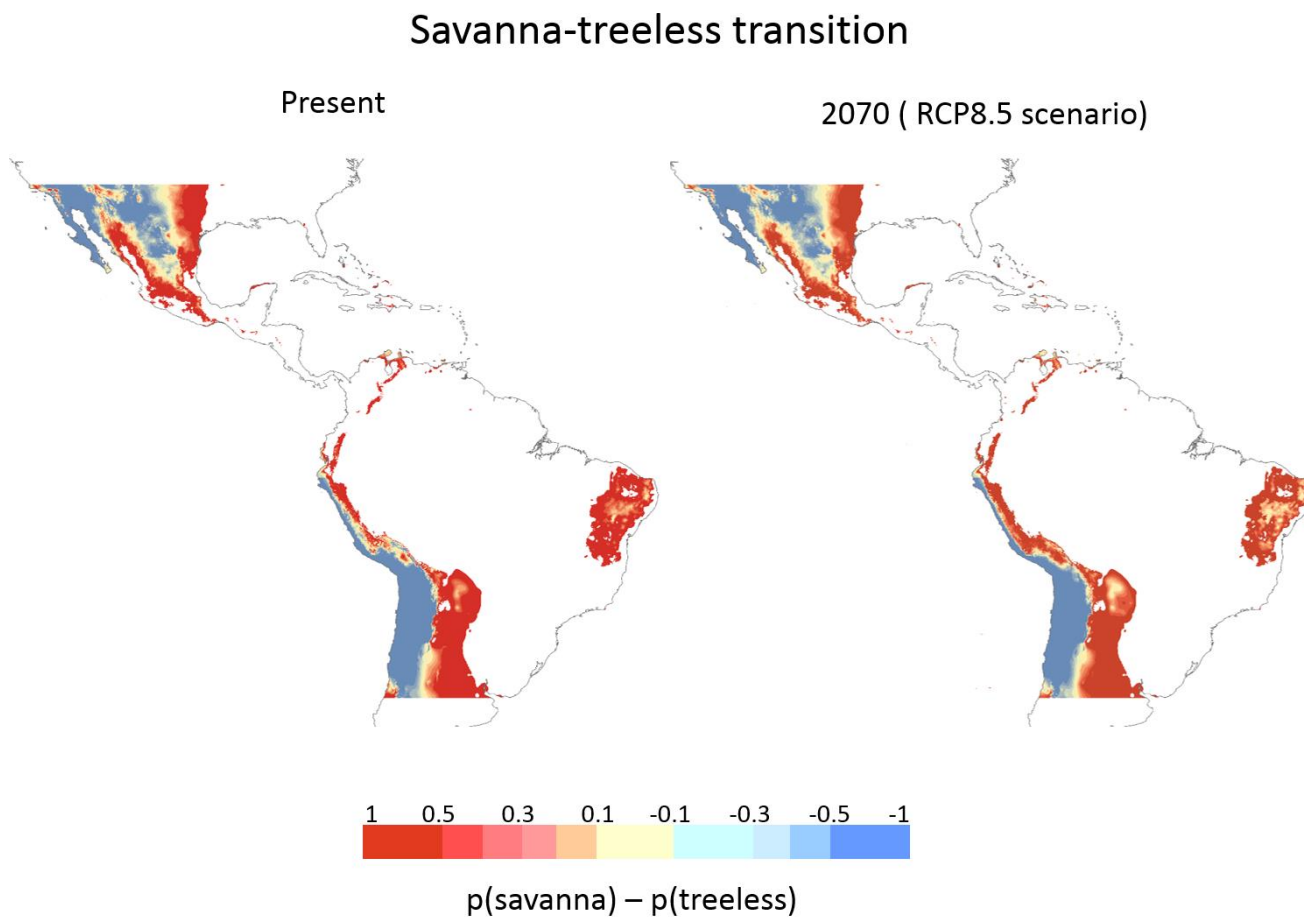
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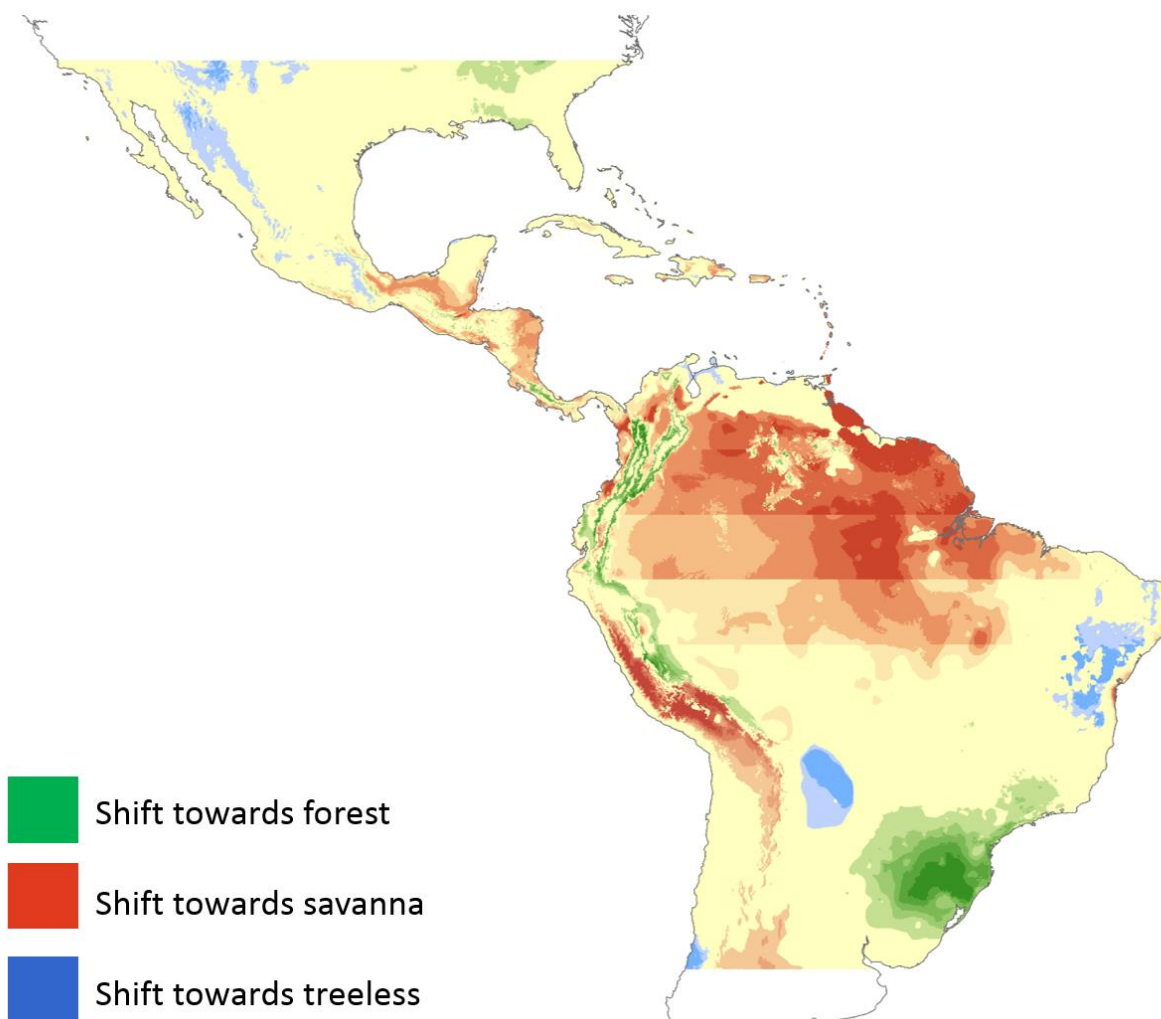
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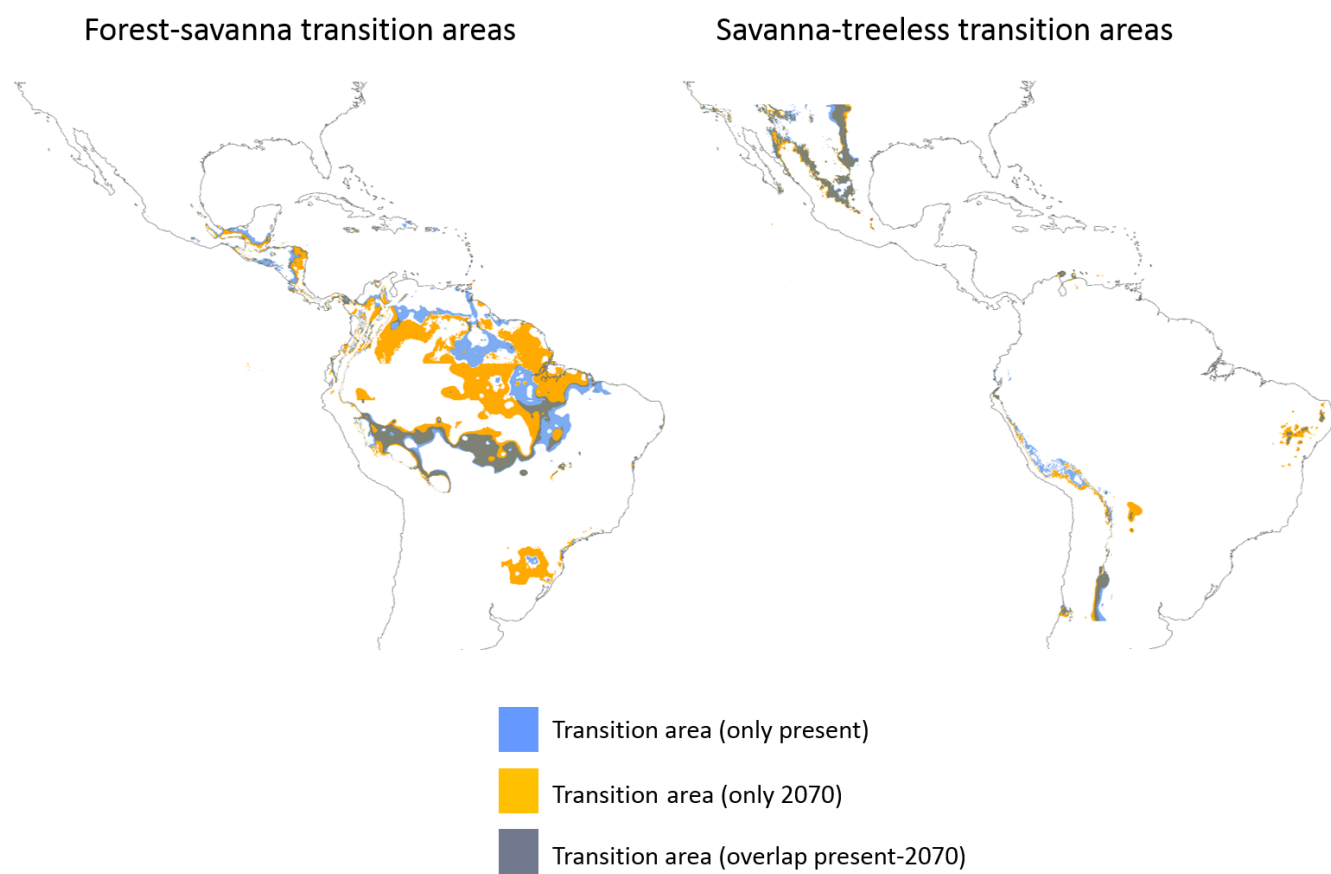
**Fig 3.**



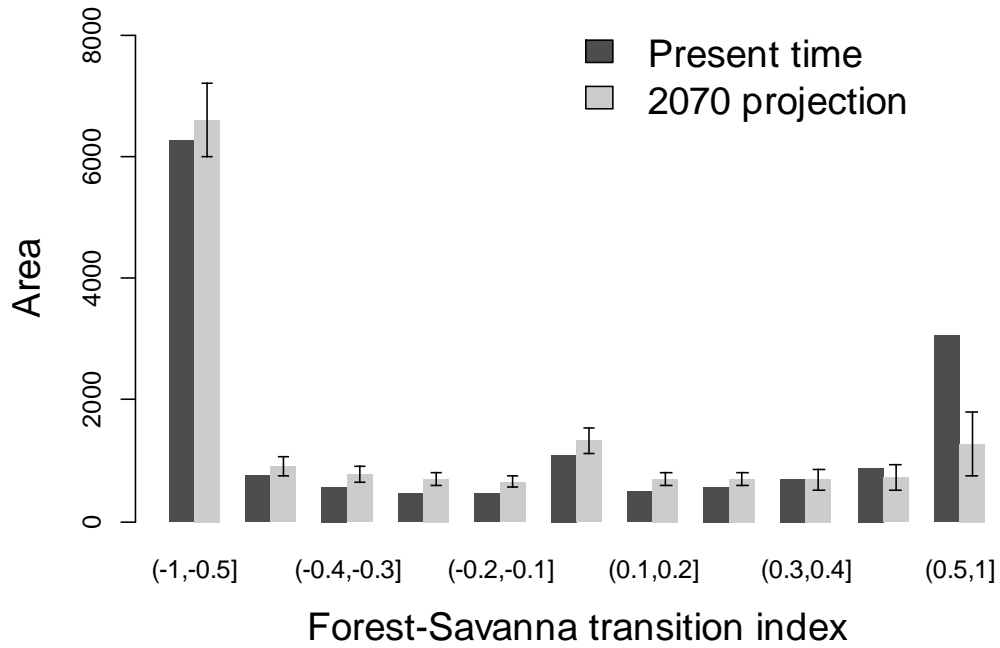
**Fig 4.**



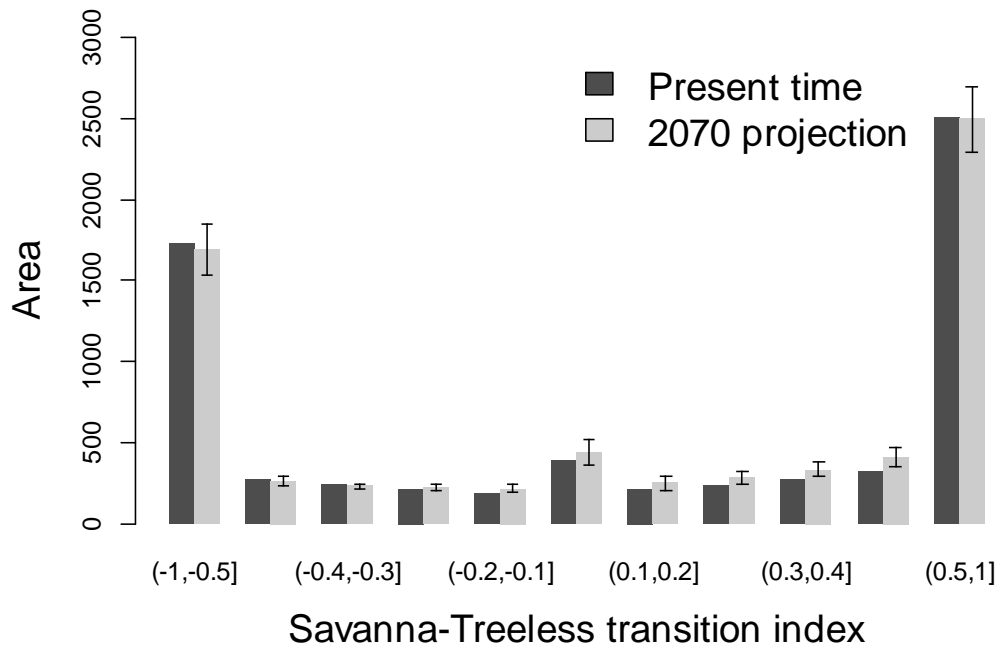
**Fig 5.**



742 **Fig 6.**



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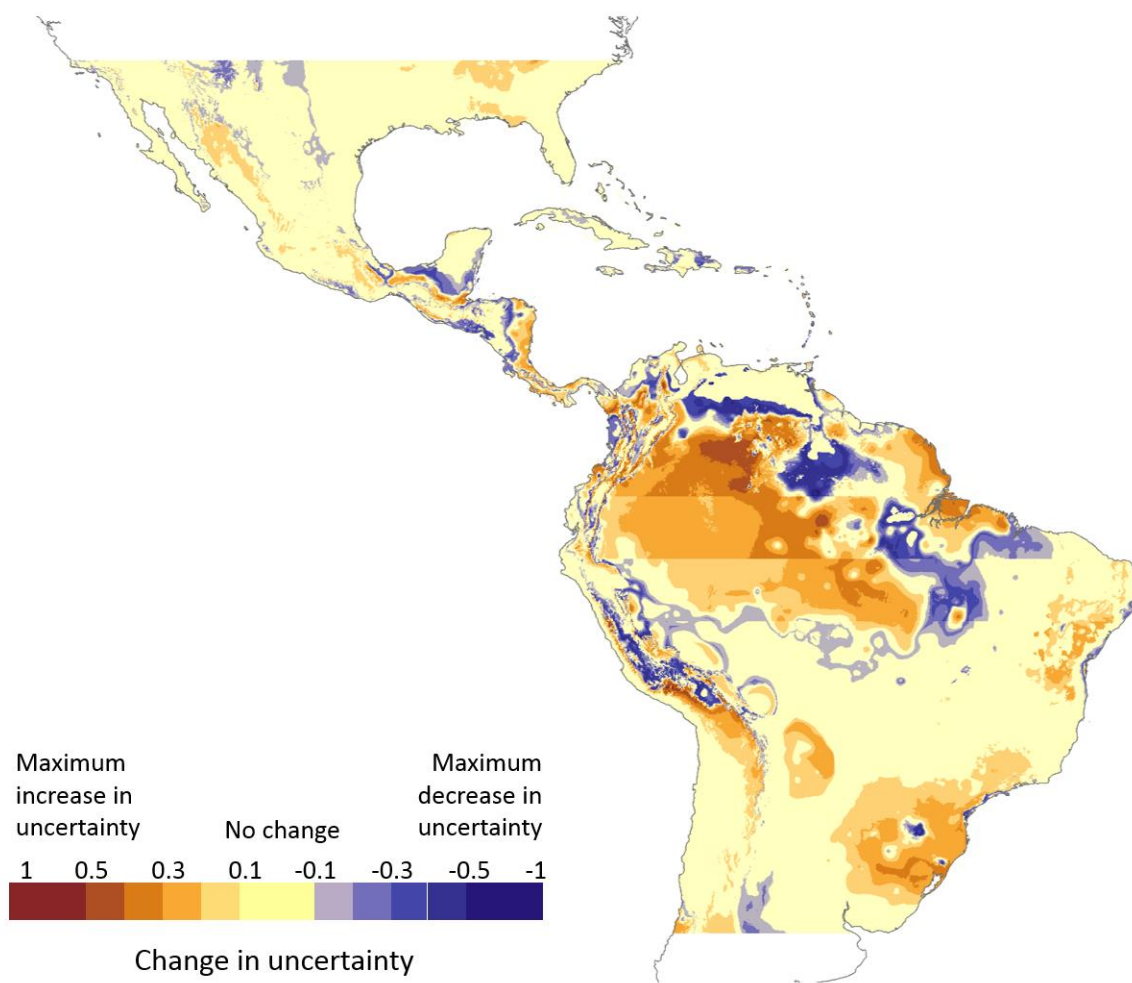
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747 **Fig 7.**

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**SUPPORTING INFORMATION**

**Table S1.** 20% best models fitted to the distribution of savanna. In all cases, the models include the same climatic variables (i.e. best global model  $P^2+T^2$ , see Table 1) plus a spatial factor. All best models included the spatial factor describing three subareas, defined by the latitudinal limits Lim1 and Lim2. Latitudinal limits for the entire study area are 35°N and -35N. The minimum latitudinal width of a subarea was 5°. For example, the model ranked first included a spatial factor with three subareas with limits: 35°N - 20°N, 20°N - -5°N and 5°N - -35°N

Rank	N subareas	Lim1	Lim2	D2	AIC
1	3	20°	-5°	33.55	2751.08
2	3	10°	-5°	33.28	2762.37
3	3	25°	-5°	31.63	2830.00
4	3	15°	-5°	32.81	2781.58
5	3	20°	0°	31.15	2849.34
6	3	10°	0°	30.26	2885.90
7	3	15°	0°	30.11	2891.87
8	3	25	0°	29.56	2914.77
9	3	5°	-5°	32.40	2798.09
10	3	20°	-10°	30.58	2872.94
11	3	30°	-5°	27.97	2979.52
12	3	25°	-10°	28.83	2944.51
13	3	20°	-15°	29.19	2929.69
14	3	5°	0°	28.99	2937.92
15	3	30°	0°	26.50	3040.08
16	3	15°	-10°	29.65	2910.80
17	3	10°	-10°	29.89	2901.21
18	3	25°	-15°	27.63	2993.68

**Table S2.** List of the 17 Coupled Model Intercomparison Project Phase 5 (CMIP5) general circulation models used in this study

Model Name	Institution ID	Modeling Center
ACCESS1-0	CSIRO-BOM	Commonwealth Scientific and Industrial Research Organization (CSIRO) and Bureau of Meteorology (BOM), Australia
BCC-CSM1-1	BCC	Beijing Climate Center, China Meteorological Administration
CCSM4	NCAR	National Center for Atmospheric Research
CNRM-CM5	CNRM - CERFACS	Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancée en Calcul Scientifique
GFDL-CM3	NOAA GFDL	NOAA Geophysical Fluid Dynamics Laboratory
GISS-E2-R	NASA GISS	NASA Goddard Institute for Space Studies
HadGEM2-AO	NIMR/KMA	National Institute of Meteorological Research/Korea Meteorological Administration
HadGEM2-CC	MOHC (additional realizations by INPE)	Met Office Hadley Centre (additional HadGEM2-ES realizations contributed by Instituto Nacional de Pesquisas Espaciais)
HadGEM2-ES	MOHC (additional realizations by INPE)	Met Office Hadley Centre (additional HadGEM2-ES realizations contributed by Instituto Nacional de Pesquisas Espaciais)
INM-CM4	INM	Institute for Numerical Mathematics
IPSL-CM5A-LR	IPSL	Institut Pierre-Simon Laplace
MIROC-ESM-CHEM	MIROC	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies
MIROC-ESM	MIROC	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies
MIROC5	MIROC	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology
MPI-ESM-LR	MPI-M	Max-Planck-Institut für Meteorologie (Max Planck Institute for Meteorology)
MRI-CGCM3	MRI	Meteorological Research Institute
NorESM1-M	NCC	Norwegian Climate Centre

**Table S3.** Predicted extent of forest, savanna and treeless areas in the tropical and subtropical Americas for 2070 under the RCP8.5 scenario for the 17 downscaled and calibrated CMIP5 global climate models (GCM). Area in  $10^3 \text{ km}^2$ . See description of climatic models in Table S2

GCM	Forest	% Forest	Savanna	%Savanna	Treeless	% Treeless
ACCESS1-0	4562	21	14568	67	2717	12
BCC-CSM1-1	4942	23	14108	65	2797	13
CCSM4	4735	22	14343	66	2769	13
CNRM-CM5	4886	22	14384	66	2577	12
GFDL-CM3	3091	14	15707	72	3049	14
GISS-E2-R	4544	21	14313	66	2990	14
HadGEM2-AO	4011	18	15292	70	2543	12
HadGEM2-CC	3882	18	15289	70	2676	12
HadGEM2-ES	4127	19	14980	69	2740	13
INM-CM4	6107	28	12848	59	2891	13
IPSL-CM5A-LR	5668	26	13010	60	3168	15
MIROC-ESM-CHEM	5493	25	13551	62	2803	13
MIROC-ESM	6397	29	12632	58	2818	13
MIROC5	5057	23	13949	64	2841	13
MPI-ESM-LR	3355	15	15569	71	2923	13
MRI-CGCM3	5306	24	13928	64	2613	12
NorESM1-M	4767	22	14001	64	3079	14



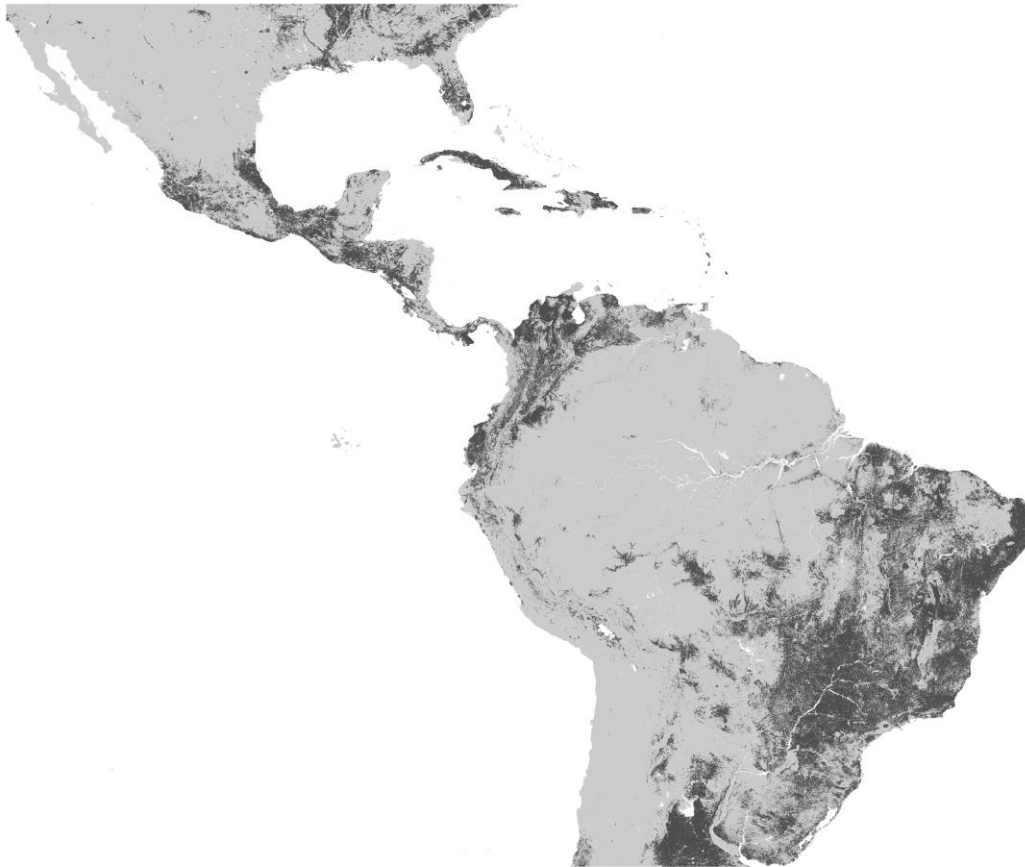
**Table S4.** Predicted extent of the classes of the Forest-savanna transition index in the tropical and subtropical Americas for 2070 under the RCP8.5 scenario for the 17 downscaled and calibrated CMIP5 global climate models (GCM). This index is calculated as  $p(\text{forest}) - p(\text{savanna})$ . Values closer to 1 indicates cells with low uncertainty of being savanna, values closer to -1 indicates cells with low uncertainty of being forest and values closer to 0 indicates high uncertainty. Mean values are shown in Figure 6 (top). See description of climatic models in Table S2. Area in  $10^3 \text{ km}^2$

GCM	(.5,1]	(.5,.4]	(.4,.3]	(.3,.2]	(.2,.1]	(.1,-.1]	(-.1,-.2]	(-.2,-.3]	(-.3,-.4]	(-.4,-.5]	(-.5,-1]
ACCESS1-0	6965	993	876	690	650	1288	663	657	716	721	1146
BCC-CSM1-1	6025	1000	962	840	678	1427	763	754	744	650	1286
CCSM4	6285	849	800	721	637	1388	661	709	620	737	1307
CNRM-CM5	6378	965	975	883	776	1598	773	681	643	797	1218
GFDL-CM3	6992	893	835	936	935	1928	760	616	291	157	331
GISS-E2-R	6890	883	854	729	635	1088	534	631	720	797	1347
HadGEM2-AO	7555	982	648	540	577	1171	554	540	623	707	997
HadGEM2-CC	7303	1099	795	653	666	1204	631	696	684	606	687
HadGEM2-ES	7364	1064	831	668	559	1239	680	689	673	739	717
INM-CM4	5940	771	651	538	488	1048	674	704	797	949	2440
IPSL-CM5A-LR	6514	689	532	540	551	1331	872	689	834	1111	1467
MIROC-ESM-CHEM	6252	933	766	629	609	1362	690	718	619	750	2014
MIROC-ESM	5423	880	759	725	723	1400	850	945	1065	1075	1744
MIROC5	6242	712	673	632	722	1401	821	822	744	697	1278
MPI-ESM-LR	7536	1288	1022	748	650	1121	579	531	459	582	643
MRI-CGCM3	6542	647	642	652	627	1366	807	906	816	726	1289
NorESM1-M	6191	859	801	680	646	1211	600	597	665	622	1692

**Table S5.** Predicted extent of the classes of the Savanna-Treeless transition index in the tropical and subtropical Americas for 2070 under the RCP8.5 scenario for the 17 downscaled and calibrated CMIP5 global climate models (GCM). This index is calculated as  $p(\text{savanna}) - p(\text{treeless})$ . Values closer to 1 indicates cells with low uncertainty of being treeless, values closer to -1 indicates cells with low uncertainty of being savanna and values closer to 0 indicates high uncertainty. Mean values are shown in Figure 6 (bottom). See description of climatic models in Table S2. Area in  $10^3 \text{ km}^2$

GCM	(.5,1]	(.5,.4]	(.4,.3]	(.3,.2]	(.2,.1]	(.1,-.1]	(-.1,-.2]	(-.2,-.3]	(-.3,-.4]	(-.4,-.5]	(-.5,-1]
ACCESS1-0	1694	217	225	205	198	350	197	248	276	354	2573
BCC-CSM1-1	1628	278	248	218	205	491	275	293	325	389	2440
CCSM4	1537	257	226	234	262	539	273	291	348	444	2788
CNRM-CM5	1483	268	230	218	203	362	206	255	292	347	2348
GFDL-CM3	1746	309	235	250	240	587	349	354	374	419	2369
GISS-E2-R	1856	254	207	207	226	497	233	230	276	333	2474
HadGEM2-AO	1495	238	213	196	192	446	268	301	356	430	2878
HadGEM2-CC	1547	269	240	240	203	381	242	278	345	405	2740
HadGEM2-ES	1692	258	246	214	171	336	205	253	273	396	2648
INM-CM4	1737	269	218	218	233	471	276	297	355	448	2373
IPSL-CM5A-LR	1990	290	260	236	206	402	221	251	326	375	2223
MIROC-ESM-CHEM	1791	245	220	206	184	357	223	248	300	348	2453
MIROC-ESM	1777	256	219	205	185	378	227	254	317	381	2130
MIROC5	1586	293	251	251	232	529	330	354	413	521	2404
MPI-ESM-LR	1846	262	220	197	211	366	185	250	369	411	2445
MRI-CGCM3	1475	211	222	255	235	468	289	356	407	531	2432
NorESM1-M	1856	272	227	231	257	485	243	293	324	435	2738

**Fig S1.** Distribution of areas undergoing human activities (categories 16-18 and 22 in the Global Land Cover 2000 (GLC2000; Bartholome & Belward, 2005) in the Tropical and Subtropical Americas (dark grey). These areas were filtered out from our analyses.



## REFERENCES

Bartholome, E. & Belward, A. S. (2005) GLC2000: a new approach to global land cover mapping from Earth observation data. *International Journal of Remote Sensing*, **26**, 1959-1977